TAXONOMY OF THE *SYMPHYOTRICHUM* (ASTER) *SUBULATUM* GROUP AND *SYMPHYOTRICHUM* (ASTER) *TENUIFOLIUM* (ASTERACEAE: ASTEREAE)

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ABSTRACT

North American and Central American taxa of *Symphyotrichum* sect. *Oxytripolium* (*S. subulatum* sensu lato and *S. tenuifolium* sensu lato) have been treated at both specific and varietal rank. As interpreted here, morphological discontinuities and reproductive isolation indicate that specific rank is appropriate for the five annual taxa, including the South American native *S. squamatum*, which is recorded primarily as a waif in the U.S.A. A key is provided to the annual taxa under consideration and summaries of synonymy are given for each. State distribution records are documented for the following: *S. subulatum*—Arkansas, Nebraska; *S. divaricatum*—New Mexico; *S. bahamense*—Georgia; *S. expansum*—Florida, Oklahoma; *S. squamatum*—Alabama, California, Florida, Louisiana, Texas.

RESUMEN

Los taxa de Norte América y América Central de *Symphyotrichum* sect. *Oxytripolium* (*S. subulatum* sensu lato y *S. tenuifolium* sensu lato) se han tratado tanto con rango especifico como varietal. Tal como se interpreta aquí, las discontinuidades morfológicas y aislamiento reproductor indican que el rango especifico es el apropiado para los cinco taxa anuales, incluyendo la nativa Sur Americana *S. squamatum*, que se cita principalmente como una planta abandonada en U.S.A. Se ofrece una clave para los taxa anuales en consideración y se hacen resúmenes de las sinonimias para cada uno de ellos. Se documenta la distribución en estados de los siguientes: *S. subulatum*—Arkansas, Nebraska; *S. divaricatum*—Nuevo México; *S. bahamense*—Georgia; *S. expansum*—Florida, Oklahoma; *S. squamatum*—Alabama, California, Florida, Texas.

Seven taxa of *Symphyotrichum* sect. *Oxytripolium* (DC.) Nesom (*Symphyotrichum* subg. *Astropolium* (Nutt.) Semple) comprise *Symphyotrichum* (*Aster*) *subulatum* (Michx.) Nesom sensu lato and *Symphyotrichum* (*Aster*) *tenuifolium* (L.) Nesom sensu lato. Six of these taxa are native primarily to North America and Central America (including the Antilles and Bahamas); one is native to South America. One or several of them occur as cosmopolitan weeds, but identifications need to be reexamined for accuracy and consistency. Sundberg (1986, 2004, 2005) has followed a broad species concept, emphasizing putative intergradation among the taxa (see comments below), and treated *S. subulatum* as a single species with five varieties and *S. tenuifolium* with two varieties. All seven of these taxa are treated here (and in Nesom 1994) at specific rank; bases for the taxonomic decisions are differences among the taxa in morphology, geography and ecology, chromosome number, self compatibility, and sterility in

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natural and experimental hybrids. Information on reproductive biology, chromosome numbers, and hybridization is from Sundberg (1986).

The observations and considerations here are predicated on the initial study and sorting of the North American oxytripolioid taxa by Sundberg (1986, 2004), who found the larger patterns in a taxonomically difficult complex and provided detailed information regarding typification. My disagreements with Sundberg are primarily in asssignments of rank, based largely on interpretation of data, as I mostly agree with his delimitation of taxa. While I have seen plants in the field and studied a large number of specimens, Sundberg collected this group widely and for his dissertation research had on hand several thousand specimens from various herbaria. The lesser intensity of the present analysis and commentary, however, does not invalidate the conclusions. The key provided below is based on Sundberg's dissertation study (1986) but has been modified as I worked through collections. Hopefully, the present overview will supplement that of Sundberg's FNA treatment (2005) in facilitating more accurate identifications of these taxa.

Documentation is provided for various distribution records, which have not been given in Sundberg's dissertation or publications. His distribution maps (1986) were small-scale and did not show U.S.A. counties. Some points of the present discussion were made earlier in brief (Nesom 1994).

Annual taxa—*Symphyotrichum subulatum* sensu lato

A map compiled by Sundberg (1986) shows that in their native (New World) ranges, the five annual taxa are discrete in geographic distribution, each almost completely allopatric with the others. In those with partially contiguous ranges, he indicated in text that intermediates occur in relatively small areas, but intermediates were not shown on the map. The taxa are morphologically distinct although by relatively small differences.

Symphyotrichum squamatum and *S. bahamense* are tetraploids ($2n = 20$), while the other taxa are diploids ($2n = 10$). Sundberg reported naturally occurring intermediates between (1) *S. bahamense* [$2n = 20$] and *S. subulatum* [$2n = 10$], (2) *S. bahamense* [$2n = 20$] and *S. expansum* [$2n = 10$], and (3) *S. divaricatum* [$2n = 10$] and *S. expansum* [$2n = 10$]. His own study, however, provided evidence regarding internal reproductive isolation among these taxa. "Artificial hybrids produced in the greenhouse among these [five] varieties are highly sterile" (Sundberg 1986, p. 63). He obtained plump achenes (presumably those that were germinable) only from crosses between *S. bahamense*-*S. divaricatum*, *S. bahamense*-*S. expansum*, and *S. expansum*-*S. squamatum*, and each of these pairings was between a diploid and tetraploid. A photo in Sundberg (1986) shows 15 mitotic chromosomes of a triploid artificial hybrid between *Symphyotrichum bahamense* and *S. expansum*.

Notwithstanding the significance of naturally occurring intermediates to

Sundberg's view of the variation patterns, he did not report the occurrence of a naturally occurring triploid plant among the 86 natural populations of annual oxytripolioid taxa from which he made chromosome counts. Nor, apparently (judging from his vouchers at TEX), did he make a chromosome count of a plant suspected of being a natural hybrid of a diploid-tetraploid parental cross. Semple (1992) noted that of 6908 chromosome counts reported for North American asters (mostly *Symphyotrichum*) and goldenrods, only 8 (0.12%) were triploid. This suggests that intergradation may not be as prevalent as Sundberg surmised, if it can be inferred from Semple's data that triploids survive at a very low frequency.

Sundberg (2004, p. 906) pointedly summarized his rationale for treatment of these taxa at infraspecific rank: "**The varieties intergrade morphologically where their distributions approach one another.**" I have been unable to corroborate this implied ubiquity of intergradation, certainly not to the extent that would suggest treating all taxa as a single species. The annual taxa appear to be essentially discrete in morphology at their points of geographic contact and overlap. Tendencies for overlapping variation in one or a few morphological features, as described by Sundberg (2004), are not necessarily the result of intergradation, which characteristically is understood to imply the existence of a zone of morphological intermediacy with continous gene exchange. Discontinuities in morphology imply the existence of reproductive isolation. Sundberg's sentence immediately following the one above suggests that his view of "intergradation" reflected a broad interpretation of that process: "**This [intergradation] may be the result of past hybridization events and limited gene flow across reproductive barriers.**"

Even with recognition that reproductive isolation exists among the annual oxytripolioid taxa, morphological differences often are subtle. Infraspecific variability and parallel variation, especially within *Symphyotrichum divaricatum* and *S. bahamense*, produce individuals that might be misidentified without an understanding of the morpho-geographic patterns. Differences among the diploid taxa, however, are clearer, and the tetraploid *S. bahamense* apparently is reproductively isolated from the three closely related diploid taxa with which it is contiguous-sympatric. The species concept underlying the present analysis emphasizes biological discontinuities.

Annual plants of sect. *Oxytripolium* adventive in Australia and various Pacific islands have mostly been identified simply as *Aster subulatus* (e.g., Walker 1976; Harden 1992; Jones 1999), although Soejima and Peng (1998) reported the occurrence of two taxa (as *A. subulatus* var. *subulatus* and *A. subulatus* var. *sandwicensis*) in Taiwan. Smith (1991) included *A. subulatus* for Fiji, noting that it probably existed only as a ballast waif. Naturalized plants from other parts of the world have been identified as *A. squamatus*, e.g. Europe (Tutin et al. 1976), Russia (Tamamschyan 1959), and Zimbabwe (Mapaura & Timberlake

2004). Where two or more of these taxa may co-occur as adventives in regions outside of their native range, observations and perspective of the present commentary suggest that they will remain morphologically discrete. For example, *S. squamatum*, *S. bahamense*, and *S. expansum* in characteristic morphology have been recorded from Japan (see below).

The name *Aster exilis* Elliott (Sketch Bot. S.Carolina 2:344. 1823) has often been applied to these plants, but as noted by Shinners (1953), a type has never been located and Elliott's description may well have applied to some form of *Symphyotrichum dumosum*. With heads on the upper branches "in racemes on peduncles two to four lines long," ray florets "twice as long as the involucrum," and occurring "in the western districts of Georgia," the plants that Elliott described could hardly be any of the annual taxa considered here.

Symphyotrichum subulatum (Michx.) Nesom, Phytologia 77:293. 1994. *Aster subulatus* Michx., Fl. Bor.-Amer. 2:111. 1803. *Symphyotrichum subulatum* var. *subulatum* (sensu Sundberg 2004). TYPE: U.S.A. "PENNSYLVANIA."

Aster subulatus var. *euroaster* Fernald & Griscom, Rhodora 37:183. 1935. TYPE: U.S.A. VIRGINIA.
Aster subulatus var. *obtusifolius* Fernald, Rhodora 16:61. 1914. TYPE: CANADA. NEW BRUNSWICK.
Aster ensifer Bosserdet, Taxon 19:250. 1970. TYPE: U.S.A. MASSACHUSETTS.

$2n = 10$. Self-compatible. Primarily outer coastal plain of the Gulf and Atlantic coasts of Canada (New Brunswick) and the eastern U.S.A. (Texas, Louisiana, Mississippi, Alabama, Florida-northeastern counties disjunct to the western panhandle region, Georgia, South Carolina, North Carolina, Virginia, Maryland, Delaware, New Jersey, Pennsylvania, New York, Connecticut, Rhode Island, Massachusetts, New Hampshire, Maine); coastal salt and brackish marshes, depressions between sand ridges, spoil banks along canals, shorelines near the coast. Also in inland marshes and saline areas of various states (Arkansas, Nebraska, Illinois, Indiana, Ohio, Michigan, and Ontario). Semple et al. (2002) noted that the species may have been introduced into Ontario only after salt mining began in the region. It was first collected in Michigan in 1914 at a salt mine and "survives now along well salted highways" (Voss 1996). In Illinois, it is "adventive along highways, rapidly spreading in ne. Ill." (Mohlenbrock 2002). Label data and photos of herbarium collections made in eight counties of the Chicago region (V Plants 2005) indicate that the plants there grow mostly in ditches and road shoulders. Collections from south-central Arkansas (citations below) are from an area apparently polluted by salt from oil drilling.

First reports for **Arkansas. Union Co.:** 5 mi S of Calion, sandy oil spill barrens, 8 Oct 1988, *Sundell 8794* (VDB); edge of bare vegetation-less area in salty runoff area from oil wells beside Union Co. Rd. 25, 1 mi N of Urbana near a branch of Richmond Creek, 22 Oct 1987, *Thomas 103,102* (NLU); salty runoff area beside small stream just E of Lawson and S end of Ark. 129, area graded in attempt to clean up runoff from oil wells, 22 Oct 1987, *Thomas 103,117* (NLU); salty area from oil well runoff beside branch of Mill Creek, 2 mi N of Old Union and Ark. 15, 7 Oct 1988, *Thomas 107,952* (NLU, TEX); 1 mi N of Urbana, salty area along a branch of Richmond Creek, beside Union Co. Rd. 25, 7 Oct

1988, *Thomas 108,025* (NLU, VDB); sandy soil in oil field N of Ark. 335 along E bank of Hayes Creek 2 mi E of Norphlet, 15 Sep 1989, *Thomas 112,871* (NLU). First reports for **Nebraska. Lancaster Co.:** just W of Lincoln, Oak Lake, plant very common along saline shore, 7 Oct 1974, *Churchill 4862* (BRIT, NLU); artificial pond by Salt Creek, N of University campus, *Shildneck C-14017* (TEX). *Symphyotrichum divaricatum* also occurs in Lancaster County (e.g., *Shildneck C-14016*, TEX).

Symphyotrichum subulatum usually is distinctive in its heads in a dense, elongate, pyramidal-paniculate arrangement (or corymbiform in small plants with relatively few heads), relatively long involucres, phyllaries without a distinct apical green zone, ray florets 1.5–2.5(–3) mm long and coiling back distally in 1/2–1 coils, disc florets 4–10(–13), accrescent pappus, and typical salt marsh habitat (the only one of the annual taxa adapted to saline substrate). Axillary heads sometimes mature as sessile to subsessile, as is characteristic of *S. bahamense*, but other features of *S. subulatum* establish its identity. It perhaps forms triploid hybrids with *S. bahamense* (fide Sundberg) but apparently is more completely isolated from the other annual taxa (see comments under *S. divaricatum*).

Symphyotrichum divaricatum (Nutt.) Nesom, Phytologia 77:279. 1994. *Tripolium divaricatum* Nutt., Trans. Amer. Philos. Soc. 2, 7:296. 1841. *Aster divaricatus* (Nutt.) Torrey & A. Gray, Fl. N. Amer. 2:163. 1841 (not *Aster divaricatus* L.). TYPE: U.S.A. MISSISSIPPI: "inundated banks of the Mississippi," collected by Thomas Nuttall, probably in December 1811, in the vicinity of Natchez, Mississippi, or around New Orleans, Louisiana (Graustein 1967).

Aster subulatus var. *ligulatus* Shinners, Field & Lab. 21:159. 1953. *Symphyotrichum subulatum* var. *ligulatum* (Shinners) Sundberg, Sida 21:907. 2004. TYPE: U.S.A. TEXAS.

Aster neomexicanus Wooton & Standley, Contr. U.S. Natl. Herb. 16:187. 1913. TYPE: U.S.A. NEW MEXICO (see citation and comments below).

$2n = 10$. Self-incompatible. Common in the south-central U.S.A. (Texas, Oklahoma, Kansas, Nebraska, New Mexico, Arkansas, Louisiana, Mississippi, Alabama, Kentucky (fide Clark et al. 2005), Tennessee, Missouri (in the southeasternmost two counties), apparently spreading eastward (e.g., Virginia; Nesom 2000) and expected to appear elsewhere along the Atlantic coastal plain. Mexico (Tamaulipas southward to the vicinity of Tampico in Veracruz, northern Coahuila, and Chihuahua, in the area of Cd. Chihuahua, Cd. Delicias, and Meoqui). Figure 1. Disturbed habitats, often moist (but usually not wet), sand, loam, and clay, common and often extremely abundant along roadsides and ditches and in lawns; in the drier Great Plains region, it occurs on lake shores, marsh and playa margins, depressions, and flats. Sometimes flowering into February.

Documentation for occurrence in **New Mexico. Chaves Co.:** Roswell, 3800 ft, Aug 1900, *Earle & Earle 327* (US, holotype of *Aster neomexicanus*; NMC isotype). **Eddy Co.:** Carlsbad Springs, *Standley 40329* (US). **Guadalupe Co.:** Los Esteros Creek, *Tschaikowsky 401* (ARIZ). The collections from Eddy and Guadalupe cos. were recorded by Sundberg on exsiccatae lists filed in herbarium TEX.

Symphyotrichum divaricatum is distinct from the other annual taxa in its relatively long and conspicuous ray florets and in its tendency to produce heads in

a diffuse arrangement (vs. sessile to subsessile axillary (*S. bahamense*), distally clustered (*S. squamatum*, *S. expansum*), or densely elongate, pyramidal-paniculate (*S. subulatum*). Before production and maturation of axillary heads, the aspect of young plants of *S. divaricatum* may resemble that of *S. bahamense*. Heads in small plants of *S. divaricatum* and in plants from Mississippi and Alabama often are produced in a corymbiform arrangement, more characteristic of *S. expansum*, but the larger heads, long-acuminate phyllaries, and much longer ray corollas indicate their identity.

Sundberg (2004) noted that *Symphyotrichum divaricatum* is "the least variable taxon" [among the annual oxytripolioids], but I observe that it is markedly variable at least in head size (inner phyllaries (4–, 4.5–)5–5.5(–6.5) mm long) and in height (plants (3–)20–100(–200, 300) cm tall). A collection from Hidalgo Co., Texas (*Cory 51331*, SMU), was noted by its collector to be of plants up to 3 meters tall, "the largest aster plant I have ever seen." Plants in lawns will continue to produce small heads even after being mowed to about 3 centimeters in height.

The combined geographic range of *Symphyotrichum divaricatum*, *S. bahamense*, and *S. expansum* is roughly doughnut-shaped, with the Gulf of Mexico as the hole—each of the three taxa occupies a major portion of the circumference. As noted below, *S. divaricatum* and *S. expansum* are slightly, intermittently sympatric at the extremities of their ranges in west Texas and adjacent Mexico (Fig. 1). The geographic ranges of *S. bahamense* and *S. divaricatum* approach each other but apparently do not make contact—the easternmost portion of the range of the latter is in southern to central Alabama, while the former reaches its westernmost point in Bay, Gulf, and Franklin cos., Fla., in the central panhandle region (Fig. 1). *Symphyotrichum bahamense* and *S. expansum* are sympatric in southernmost Florida.

The geographic range of *Symphyotrichum divaricatum* closely approaches that of *S. subulatum* in places along the Gulf Coast. Plants of *S. divaricatum* even grow to terrestrial edges of marsh and deeper water along the coast, but habitats of the two taxa are distinct and they appear to be completely reproductively isolated.

Representative coastal localities for *Symphyotrichum divaricatum* (closely approaching habitats of *S. subulatum*). **Alabama. Mobile Co.:** Battleship Park, brackish moist sands, 22 Oct 1969, *Kral 38290* (VDB); E of Theodore in Deer River area, sandy open dock area (Navy) along Mobile Bay, 25 Oct 1999, *Kral 89064* (NLU, VDB). **Louisiana. Vermilion Par.:** Redfish Point, W side of Vermilion Bay, vicinity USL field station, scattered in marsh (brackish) [growing near *Symphyotrichum subulatum*], 28 Oct 1961, *Reese 5726* (VDB). **Texas. Jefferson Co.:** 3.5 mi SW of Port Arthur, moist places of coastal flats, 18 Nov 1945, *Cory 50949* (SMU); 10 mi W of Sabine Pass on Hwy 87, sand above intertidal zone, 19 Nov 1968, *Mahler 5175* (SMU). Locality for *Symphyotrichum subulatum* sensu stricto sympatric (as noted on label) with *S. divaricatum*. **Mississippi. Jackson Co.:** Pascagoula, vic. Bayou Casotte, S of jct of Louise St. and Washington Ave., heavily disturbed fill area, clay soil with oyster fragments, growing within 100 yds of *Aster subulatus* var. *ligulatus*, 5 Nov 1994, *MacDonald 8179* (VDB).

See further comments following *S. expansum*.

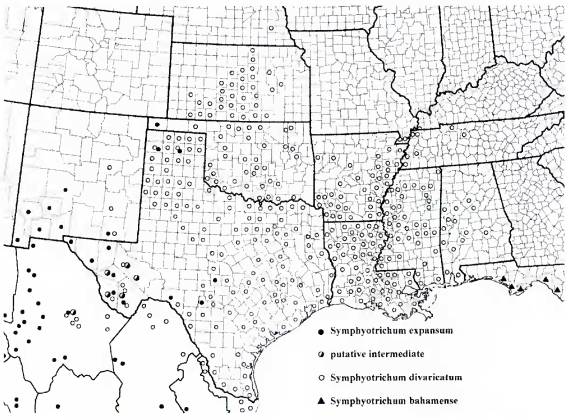

FIG. 1. Geographic distribution of *Symphyotrichum divaricatum*. Also shown are the eastern approach of *S. bahamense* in the Florida panhandle and the western approach and sympatry of *S. expansum*. U.S.A. records for *S. divaricatum* are from BRIT-SMU, MO, NLU, NMC, OKL, TEX-LL, VDB, and various sources of literature; a few (as cited) are from Sundberg (1986). Records for *S. expansum* in Mexico are from TEX-LL and from various other herbaria, accumulated in a yet unpublished taxonomic treatment (Nesom) of Mexican Astereae. Records for *S. bahamense* are from USF and VDB.

Symphyotrichum bahamense (Britton) Nesom, Phytologia 77:276. 1994. *Aster bahamensis* Britton, Bull. Torrey Bot. Club 41:14. 1914. *Aster subulatus* var. *bahamensis* (Britton) Bosserdet, Taxon 19:249. 1970. TYPE: BAHAMAS: GRAND BAHAMA.

Aster subulatus var. *elongatus* Bosserdet ex Jones & Lowry, Adansonia, ser. 4, 8:406. 1986 (not Bosserdet, Taxon 19:250. 1970, nom. invalid., without designation of a type). *Symphyotrichum subulatum* var. *elongatum* (Bosserdet ex Jones & Lowry) Sundberg, Sida 21:907. 2004. TYPE: U.S.A. FLORIDA.

$2n = 20$. Self-compatible. From the eastern portion of the Florida panhandle throughout most of peninsular Florida to the Keys (43 counties recorded for Florida in this study); also in a few localities of coastal Georgia and in the Bahama Islands (including the type). Hispaniola: Santo Domingo, 25 Oct 1929, *Ekman 13918* (LL); Alain (1962) included *S. bahamense* in the flora of Cuba. Japan: Chiba Pref., Futtsu City, abandoned rice paddy, 8 Oct 1985, *Enomoto s.n.* (TEX). Ditches and depressions, pond edges, edge and upper part of salt marsh, fresh water marsh, fields, grassy roadsides, lawns, disturbed sites, woods edges.

Documentation for occurrence in **Georgia. Glynn Co.**: ca. 0.4 mi S of E end of bridge of Jekyll Island,

upper part of salt marsh, 25 Oct 1975, *Duncan 29660* (VDB); ca. 1.7 mi NW of St. Simons, higher part of salt marsh, 17 Sep 1971, *Duncan 23665* (VDB); exposed, low roadside at Super 8 Motel, 23 Oct 2001, *McNeilus01-339* (NLU). **McIntosh Co.:** ca. 2.4 mi due N of southern tip of Sapelo Island, marshy area, usually fresh water, just back of narrow strip of oaks along Duplin River, 14 Oct 1956, *Duncan 20635* (BRIT, TEX).

Symphyotrichum bahamense is characterized by its distinctive arrangement of heads (at first at ends of long, bracteate branches, then produced and maturing as axillary and nearly sessile or on very short lateral branches, commonly appearing secund to subsecund) and ray corollas mostly 2–3.5(–4) mm long, with blue to purple laminae coiling back in 2–3 coils. The ray corollas are shorter than in *S. divaricatum* and the disc florets fewer.

According to Sundberg (1986), intermediates between *Symphyotrichum bahamense* and *S. subulatum* "occur sporadically" in Florida on northern extremities of the range of the former (Duval Co. and along the coast of the panhandle region). He noted (2004, p. 907) that "Intergradation [with *S. subulatum*] is demonstrated in the compactness of the capitulescence and the number of disk and ray florets." Such putative intermediates do not appear to be common, however, and F1's would be triploid and sterile (Sundberg 1986). There is no specimen at TEX indicated to be such a hybrid.

Putative intergradation between *Symphyotrichum bahamense* and *S. expansum* in southern Florida was noted by Sundberg (2004, p. 907) to be evidenced by "individuals of [*S. expansum*] ... more robust (to 1.5 m tall) than elsewhere and [with] the ligules ... often pink, instead of white." If any of these putative intermediates are *S. bahamense-expansum* hybrids, the F1's would be triploid and sterile. Plants of *S. bahamense* from southern Florida have a tendency for early heads to develop on relatively shorter peduncles in a corymboid arrangement; these have the general appearance of *S. expansum* but can be identified as *S. bahamense* by their larger involucres and larger, blue to purple ray florets (examples: Hendry Co: *Brass 33406*, USF; Levy Co: *Semple 3966*, USF), and the later (axillary) heads tend to be sessile or short-pedunculate, more like typical *S. bahamense*. The couplet below give details of differences.

Heads at first at ends of long, bracteate branches, then produced and maturing as axillary and nearly sessile or on very short lateral branches, commonly on one side of the main stem and appearing secund to subsecund, in paniculiform arrangements; inner phyllaries 5–6.5 mm long; ray florets in 2–3 series, laminae blue to purple, (2–)2.5–4 mm long and 0.2–0.4 mm wide (dried), coiling back in 2 or more coils; disc florets 11–23 ____ **Symphyotrichum bahamense**

Heads usually corymbiform to thyrsiform in arrangement (borne primarily on distal branches, distally clustered); inner phyllaries 4–5.5 mm long; ray florets in 1(–2) series, laminae white to light pinkish or slightly blue, 2–3 mm long and 0.1–0.3 mm wide (dried), remaining straight or coiling back in 1–2 coils; disc florets (6–)8–15 ____ **Symphyotrichum expansum**

Sundberg (1986) suggested that the tetraploid *Symphyotrichum bahamense* may have had an alloploid origin, with parents the diploids *S. divaricatum* and either

S. expansum or *S. subulatum*. Such an origin would account for at least some aspects of morphological intermediacy in *S. bahamense*.

Symphyotrichum expansum (Poepp. ex Spreng.) Nesom, Phytologia 77:281. 1994.
Erigeron expansus Poepp. ex Spreng., Syst. Veg. 3:518. 1826. TYPE: CUBA.

Aster inconspicuus Less., Linnaea 5:143. 1830. *Aster exilis* var. *inconspicuus* (Less.) Hieron., Engl. Bot. Jahrb. 29:19. 1900. TYPE: CUBA: homotypic with *Erigeron expansus*.

Erigeron multiflorus Hook. & Arn., Bot. Beechey Voy. 87. 1832. TYPE: U.S.A. HAWAII. Synonymy fide Jones (1984).

Tripolium subulatum (Michx.) DC. var. *parviflorum* Nees, Gen. sp. Aster. 157, 286. 1833. *Symphyotrichum subulatum* var. *parviflorum* (Nees) Sundberg, Sida 21:907. 2004. TYPE: U.S.A. HAWAII: as lectotypified by Sundberg (2004); homotypic with *A. divaricatus* var. *sandwicensis*.

Tripolium subulatum (Michx.) DC. var. *cubense* DC., Prodr. 5:254. 1836. *Aster subulatus* var. *cubensis* (DC.) Shinners, Field & Lab. 21:161. 1953. TYPE: CUBA: homotypic with *Erigeron expansus*.

Aster divaricatus (Nutt.) Torr. & A. Gray var. *sandwicensis* A. Gray, Proc. Amer. Acad. Arts 7:173. 1867. *Aster sandwicensis* (A. Gray) Hieron., Bot. Jahrb. Syst. 29:20. 1901. *Aster subulatus* var. *sandwicensis* (A. Gray) A.G. Jones, Brittonia 36:465. 1984. TYPE: U.S.A. HAWAII: as lectotypified by Jones (1984). Jones (1984) lectotypified *Aster sandwicensis* and interpreted it to represent the taxon identified here as *S. squamatum*. Sundberg followed this interpretation in 1986, but later (2004) decided that the type is correctly identified as *S. expansum*, in the sense of the present study.

Aster pauciflorus Nutt. var. *gracilis* Benth. ex Hemsley, Biol. Centr. Amer. Bot., 122. 1881. TYPE: COSTA RICA. Synonymy fide Sundberg (1986).

Aster exilis Elliott var. *australis* A. Gray, Synopt. Fl. N. Amer. 1(2):203. 1884. *Aster subulatus* var. *australis* (A. Gray) Shinners, Field & Lab. 21:158. 1953. TYPE: U.S.A. HAWAII: homotypic with *A. divaricatus* var. *sandwicensis*.

Aster madrensis M.E. Jones, Contr. Western Bot. 12:43. 1908. TYPE: MEXICO. CHIHUAHUA.

$2n = 10$. Self-compatible. Moist or wet places, southwestern USA (Texas, New Mexico, Oklahoma, Arizona, California, Nevada, Utah), Florida (southernmost counties and other scattered localities), Mexico (all states, including southern Tamaulipas, Nuevo León, Coahuila, Chihuahua, and Sonora), Central America (Guatemala, Belize, Nicaragua, Costa Rica), Antilles (Jamaica, Hispaniola-D.R.). Hawaii, Japan: Okayama Pref., Kasaoka City, on newly reclaimed land at Kasaoka Bay Polder, 14 Sep 1984, *Enomoto s.n.* (TEX).

First report for **Oklahoma. Cimarron Co.:** along a small creek ca. 7 mi E of Kenton, 25 Sep 1976, *J. Taylor 23717* (BRIT). Cimarron County is the western extremity of the Oklahoma panhandle, relatively close to the Texas panhandle localities in Hartley and Hutchinson cos., cited below.

Disjunct localities in **Texas. Hartley Co.:** sandy soil along Punta de Agua Creek, between Romero and Middle Water, in water of stream, 9 Oct 1964, *Correll 30339* (LL, SMU). **Hutchinson Co.:** Lake Meredith Natl. Rec. Area, Spring Creek picnic and fishing area around small lake and adjacent marsh area, NE side (immediately downstream) of Sanford Dam, in water of ditch beside marsh, 20 September 2002, *Nesom & O'Kennon 853* (BRIT). **Mason Co.:** 5 air mi NNW of Mason, 2.1 mi N of jct. of Hwy 29 and Hwy 398,; then 2.4 mi NW on dirt road, 24 Sep 1999, *Singhurst 8248* (TEX). **Real Co.:** Dry Creek, 0.1 mi S of (downstream from) mouth of Javelina Creek, ca. 800-1000 ft. N of Dry Creek Rd. (Lost Canyon Rd.) from a point 4.0 roadmiles E of its jct. with St. Rt. 55 at Barksdale, elev. ca. 1650 ft., W shoreline of pond, 3 Oct 1998, *Carr 17771* (TEX). **Val Verde Co.:** Pecos River at Highway 90, S of the high bridge of Hwy 90, along the E bank of the Pecos, locally abundant, 9 Nov 1999, *Henrickson 22624* (TEX).

Representative documentation for **Florida. Collier Co.:** Vic. of Naples, S of town, common in marshy ditch, 9 Oct 1962, *Cooley 9028* (USF). **Dade Co.:** Perrine, empty, oolitic lot, 19 Sep 1973, *Kral 51893* (VDB). **Lake Co.:** Eustis-Trout Lake Nature Center, 1 Oct 1991, *Daubenmire s.n.* (USF). **Monroe Co.:** Big Pine Key, Sands subdivision, 8 Sep 1981, *Brumbach 9729* (BRIT, USF-2 sheets); Marathon Key, near intersection of Hwy 1 with 37th Street, roadside fill, 11 Nov 1983, *Sundberg 2327* (TEX) and *2328* (TEX); Key Largo, 0.2 m S of Tavernier Creek along Hwy 1, roadside fill, 11 Nov 1983, *Sundberg 2329* (TEX). **Okaloosa Co.:** Eglin Air Force Base, grassy area around pond just S of Eglin Blvd, along 7th St., 21 Nov 1983, *Wilhelm 11929* (USF).

Symphyotrichum expansum is recognized by its relatively small heads distally clustered in a corymbiform to thyrsiform arrangement and short (but still coiling at maturity), whitish to pinkish or light blue ray florets about as long or slightly shorter (in coiled form) than the pappus. Among the annual taxa, it is the most geographically widespread and elevationally diverse. In the western U.S.A. and Mexico, typical *S. expansum* occurs at 100–1650(–1950) meters; from Central America to Florida, it rarely grows at more than 10 meters.

The range of *Symphyotrichum expansum* apparently slightly overlaps that of *S. divaricatum* in southeastern New Mexico, western Texas, and adjacent Mexico. For the most part, the two are clearly distinct, and attempts by Sundberg (1986) to cross these two diploid taxa produced 0–3% plump achenes, almost all of which were inviable. In a yet unpublished floristic study in the Texas panhandle region (Hutchinson Co.), typical *S. expansum* has been observed in close proximity, without intermediacy, to typical *S. divaricatum*; the latter is an abundant colonizer in the sandy clay at many sites of the fluctuating shoreline of Lake Meredith (e.g., *Nesom & O'Kennon 689*, as cited above), while *S. expansum* was observed in the muck of a wet ditch and marsh margin at only one area immediately below the dam (*Nesom & O'Kennon 853*, BRIT). In Presidio Co., Texas (Big Bend Ranch State Natural Area), the two taxa have been observed and collected in close proximity, without evidence of intergradation: *S. divaricatum* (*Worthington 22636*, TEX, UTEP) and *S. expansum* (*Worthington 22637*, TEX, UTEP). Worthington noted by annotation that he observed two species of 'aster' in BBRSNA. Pringle apparently observed two co-occurring entities in Chihuahua, on the "wet banks of the Sacramento River [vicinity of Cd. Chihuahua], 13 Sep 1886": *Pringle 751* (LL) is *S. divaricatum* while *Pringle 750* (LL) is *S. expansum*.

Even though it appears that some degree of reproductive isolation exists between *Symphyotrichum divaricatum* and *S. expansum*, Sundberg (2004, p. 906) noted that "Populations intermediate in ligule length and width occur in trans-Pecos Texas, parts of New Mexico (including the type of *Aster neomexicanus*, collected in Chaves Co.), Arizona, and Chihuahua, Mexico." My observations corroborate the existence of plants with longer and slightly wider rays, which also are blue to purple, in contrast to the smaller, white to pink rays of *S. expansum*. Most of these occur where the two species are sympatric and apparently are relatively uncommon, compared to the parents. Such putative

intermediates are similar to *S. expansum* in their small heads (inner phyllaries mostly 4–4.5 mm long) all strongly distally disposed on wiry peduncles. Because of its relatively large ray corollas, the Chaves Co. collection is identified and mapped here as typical *S. divaricatum*,, although in habit it resembles *S. expansum*.

Collections examined (*Symphyotrichum divaricatum*<?>*expansum*). **U.S.A. Texas. Brewster Co.:** 3.5 S of Marathon, infrequent in mud at Pena Blanca spring, 21 Oct 1946, *Warnock 46587* (SMU, TEX). **Jeff Davis Co.:** gravel and sand bars of Limpia Creek near Ft. Davis, 8 Oct 1926, *Palmer 23123* (TEX). **Pecos Co.:** roadside along irrigation ditch near Farm Road 1053, 1/2 mi N of Imperial, chromosome number *n*=5, 20 Aug 1967, *Watson 147* (TEX); ca. 5 mi W of Fort Stockton along IH-10, moist ditch along frontage road S of freeway, chromosome number *n*=5, 26 Aug 1983, *Sundberg 2160* (TEX). **Presidio Co**: infrequent at spring near Rex Ivy's Lodge above La Jitas, 2200 ft, 24 Sep 1961, *Warnock 18163* (TEX). **Reeves Co.:** Hwy 285, S of Pecos, 20 Aug 1941, *Strandtman s.n.* (TEX). **Mexico. Chihuahua:** Delicias, along ditch, 10 Oct 1957, *Knobloch 631* (SMU).

The broad distributions and distinct morphology of *Symphyotrichum divaricatum* and *S. expansum*, their overlap and co-occurrence in a relatively small zone of sympatry, and the relatively few putative intermediates are taken here as rationale for treating both of them at specific rank.

Symphyotrichum squamatum (Spreng.) Nesom, Phytologia 77:292. 1994. *Conyza squamata* Spreng., Syst. Veg. 3:515. 1826. *Aster squamatus* (Spreng.) Hieron., Bot. Jahrb. Syst. 29:19. 1901. *Conyzanthus squamatus* (Spreng.) Tamamsch., Fl. U.R.S.S. 25:186. 1959. *Symphyotrichum subulatum* var. *squamatum* (Spreng.) Sundberg, Sida 21:908. 2004. TYPE: URUGUAY. MONTEVIDEO.

Erigeron semiamplexicaule Meyen, Reise 1:311. 1834. TYPE: ?. Synonymy fide Cabrera (1978).

Baccharis asteroides Colla, Mem. Reale Accad. Sci. Torino 38:14, pl. 25. 1835. *Aster asteroides* (Colla) Rusby, Mem. Torrey Bot. Club 4:213. 1895. TYPE: CHILE. Synonymy fide Sundberg (1986).

Conyza berteroana Phil., Linnaea 28:737. 1836. TYPE: CHILE. Synonymy fide Sundberg (1986).

Tripolium conspicuum Lindley ex DC., Prodr. 5:254. 1836. *Aster bangii* Rusby [nom. nov.], Mem. Torrey Bot. Club 4:213. 1895. TYPE: CHILE. Synonymy fide Sundberg (1986).

Aster linifolius Griseb., Abhand. Königl. Gesellsch. Wissens. Göttingen 24:178. 1879. TYPE: ? Synonymy fide Cabrera (1978).

Aster subtropicos Morong, Ann. New York Acad. Sci. 7:139. 1893. TYPE: PARAGUAY. Synonymy fide Sundberg (1986).

Tripolium moelleri Phil., Anal. Univ. Chile 87:403. 1894. *Aster moelleri* (Phil.) Reiche, Anal. Univ. Chile 109:338. 1901. TYPE: CHILE. Synonymy fide Cabrera (1978).

Tripolium oliganthum Phil., Anal. Univ. Chile 87:403. 1894. TYPE: CHILE. Synonymy fide Cabrera (1978).

Erigeron depilis Phil., Anal. Univ. Chile 87:417. 1894. TYPE: CHILE. Synonymy fide Cabrera (1978).

Aster barcinonensis Sennen, Bull. Acad. Int. Geogr. Bot. 23:242. 1914. TYPE: SPAIN. Synonymy fide Sundberg (1986).

$2n = 20$. Self-compatible. Native to South America and apparently widely distributed there; rare in California and the southeastern U.S.A. (Alabama, Florida, Louisiana, Texas), apparently mostly as a waif, usually on or near beaches and ballast dumps. Naturalized in Australia(!), Japan(!), Iraq(!), Africa(!), France(!), and probably other regions of the world. Noted by Britton (1914) to occur on Ireland Island and Boaz Island, Bermuda.

Documentation for U.S.A. occurrences. **Alabama. Mobile Co.:** sandy W end of Dauphin Island, 18 Oct 1973, *Taylor and Taylor 15382* (BRIT); Dauphin Island, Itasca Pl. near Iberville Dr., roadside near dunes, 9 Aug 1965, *Deramus D752* (VDB); Battleship Park, by Mobile-Baldwin Co. causeway, abundant on moist brackish sands, 22 Oct 1969, *Kral 38282* (NLU). **California. Kern Co.:** S of Greenfield, intersection of Cottonwood Rd and Buena Vista Rd, along roadside ditch, 16 Apr 1983, *Sundberg 2093*, "this population $n = 10$ pairs" (TEX). **Florida. [Escambia Co.]:** Pensacola, waste ground, 27 Jul 1899, *Curtiss 6497* (GH [fide Shinners 1953], USF); **Franklin Co.:** Apalachicola, ballast weed, Jul 1897, *Chapman s.n.* (MO [fide Shinners 1953], SMU). **Louisiana Orleans Par.:** weedy areas along streets N of New Orleans Convention Center from Howard Street W to elevated hwy in New Orleans, 10 Nov 1991, *Thomas 126,773* (NLU). **Texas. [Galveston Co.]:** "Galveston, sandy beaches, damp sands along the streets, 8 Aug 1902, *J. Reverchon 3319*" (MO, US-2 sheets); the MO collection was cited by Shinners (1953) as *Aster subulatus* var. *australis*, it was identified as *Symphyotrichum squamatum* by Sundberg (1986) and Nesom (1994).

Symphyotrichum squamatum is recognized by its corymbiform to thyrsiform arrangement of heads (borne primarily on bracteate distal branches and distally clustered), inner phyllaries 5–5.5 mm long, with sharply delimited apical green zones, and ray florets numerous (21–28(–38)) with filiform, erect (non-coiling) corollas shorter (1.3–2 mm long) than the mature pappus. It is the only one of the taxa treated here that is not a North American native; its evolutionary relationship to the others may be correspondingly distant. Natural hybridization has not been reported between *S. squamatum* and any other taxon.

KEY TO THE ANNUAL TAXA

1. Heads usually dense in an elongate, pyramidal-paniculate arrangement; inner phyllaries 6–7 mm long, phyllary apices linear-acuminate, distal margins often inrolled/involute, green zone of phyllaries narrowly lanceolate, usually extending the entire length of the phyllary, chartaceous bases short or absent; pappus accrescent, 4–5.5 mm long at maturity and usually longer than coiled ray corollas; habitats wet, saline _____ **Symphyotrichum subulatum**

1. Heads corymbiform to thyrsiform, diffusely paniculate, or secund to subsecund and paniculiform arrangements or at the tips of long, bracteate branches; inner phyllaries 4–6.5 mm long, phyllary apices acute to acuminate, distal margins inrolled/involute or not, green zone of phyllaries lanceolate to elliptic, chartaceous bases usually conspicuous; pappus not accrescent, 3.5–4(–5) mm long at maturity, longer or shorter than ray coroilas; habitats moist to wet, rarely saline.
   2. Phyllary tips appressed, acute, flat, inner phyllaries with broadly lanceolate, distinctly demarcated, apical green zone, proximal 1/2–1/3 white-chartaceous; ray floret laminae erect, often involute along the edges (curling inward lengthwise), rarely coiling back distally (if so, then only ca. 1/2 coil), usually shorter than mature pappus; disc florets (3–)7–14 _____ **Symphyotrichum squamatum**
   2. Phyllary tips loose, linear-acuminate, distal margins often inrolled/involute, inner phyllaries with narrowly lanceolate, often weakly demarcated apical green zone, white-chartaceous bases short, ca. 1/3–1/2 the length of the phyllaries; ray floret laminae not involute along edges, usually coiling back distally in 1–4 or more coils, usually as long or longer than mature pappus; disc florets (6–)8–15, 11–23, or (20–)33–45(–50).
      3. Heads usually corymbiform to thyrsiform in arrangement (borne primarily on

distal branches, distally clustered); inner phyllaries 4–5.5(–6) mm long, phyllary apices acute to abruptly short-acuminate or long-acuminate, distal margins inrolled/involute or not; ray florets in 1(–2) series, corollas 2–3 mm long, laminae 0.1–0.3 mm wide (dried), white to light pinkish or slightly blue, coiling back in 1–2 coils or less commonly remaining straight; disc florets (6–)8–15 ____ **Symphyotrichum expansum**

3. Head arrangements diffusely paniculiform to pyramidal-paniculiform to corymbiform or secund to subsecund and paniculiform; inner phyllaries 5–6.5 mm long; phyllary apices long-acuminate, distal margins usually inrolled/involute; ray florets in 1–3 series, corollas 2–7 mm long, laminae 0.2–0.8 mm wide (dry), white to blue or puple, coiling back in 2–4 or more coils; disc florets 11–23 or (20–)33–45(–50).
    4. Heads often at ends of long, bracteate branches, axillary heads usually maturing on elongate lateral branches, the whole arrangement often diffusely paniculiform to pyramidal-paniculiform, or heads more distally disposed and the arrangement corymbiform to thyrsiform; ray florets in 1 series, corollas mostly 4–7 mm long, laminae 0.4–0.8 mm wide (dry), blue to white, coiling back 3–4 or more times; disc florets (20–)33–45(–50); south-central U.S.A., extreme northwestern Mexico ____ **Symphyotrichum divaricatum**
    4. Heads at first at ends of long, bracteate branches, then produced and maturing as axillary and nearly sessile or on very short lateral branches, commonly on one side of the main stem and appearing secund to subsecund, in paniculiform arrangements; ray florets in 2–3 series, corollas mostly 2–3.5(–4) mm long, laminae 0.2–0.4 mm wide (dry), blue to purple, coiling back in 2–3 coils; disc florets 11–23; Florida, coastal Georgia, Bahamas ____ **Symphyotrichum bahamense**

Perennial taxa—*Symphyotrichum tenuifolium* sensu lato

Symphyotrichum tenuifolium sensu stricto and *S. bracei* (*S. tenuifolium* var. *aphyllum*) are diploid, rhizomatous perennials endemic to coastal and near-coastal habitats. The former occurs mostly in marshes of western Cuba, the Bahamas, and the west coast of southern and central Florida; *S. tenuifolium* occurs in marshes along the Gulf coast from Texas to panhandle Florida and then along the Atlantic coast from northeastern Florida northward as far as Rhode Island, New Hampshire, and Maine. The key by Sundberg (2004) separates the two perennial taxa in a number of features. Each of them has been treated at specific rank by regional botanists (Cronquist 1980; Wunderlin 1982, 1998; Wunderlin & Hansen 2004), but Long (1970), Long and Lakela (1971), and Sundberg (1986, 2004) have regarded *S. bracei* as a variety within a more broadly conceived species. In the initial description of var. *aphyllum*, Long (1970, p. 41) noted that it is "connected by intermediate forms" to var. *tenuifolium* and is "a West Indian-Florida population segregate of the more northern [*S. tenuifolium*]." Sundberg (1986, 2004) observed that the two taxa intergrade where their ranges overlap along the Gulf Coast of northern and central peninsular Florida, from Taylor to Pinellas counties, where "almost all specimens are intermediate," suggesting that parental forms apparently are absent or rare and that gene flow is

continuous. In contrast, I find that typical *S. bracei* occurs northward well into the range of typical *S. tenuifolium* (e.g., Hernando Co., *S. bracei*, *Sundberg 2305*, TEX; Citrus Co., *S. bracei*, *Schmid A-6*, USF; Taylor Co., *S. bracei*, *Godfrey 61659*, BRIT). Sundberg (2004) scored *Godfrey 61659* (FSU) as typical of *S. bracei* except for root structure, which is lacking on the BRIT duplicate.

Species-rank concepts of Cronquist, Wunderlin and Hansen, and the present study emphasize the distinctive morphologies of the two taxa, their mostly allopatric ranges, and the apparent hybridization and intermediacy that occurs within only a relatively small area of overlap. Long and Sundberg have emphasized the zone of intermediacy as rationale for treating these two taxa as geographic segments of a single species. Whichever point of view is adopted, treatment of these at specific rank may be more subjective than for the annual taxa, where reproductive isolation apparently is stronger.

Symphyotrichum tenuifolium (L.) Nesom, Phytologia 77:293. 1994 (1995). *Aster tenuifolius* L., Sp. Pl. 2:873. 1753. TYPE: U.S.A. "in America septentrionale."

Symphyotrichum bracei (Britton ex Small) Nesom, Phytologia 77:276. 1994. *Aster bracei* Britton ex Small, Fl. Miami 190, 200. 1913. TYPE: BAHAMAS. NEW PROVIDENCE.

Aster tenuifolius var. *aphyllus* R.W. Long, Rhodora 72:40. 1970. *Symphyotrichum tenuifolium* (L.) Nesom var. *aphyllum* (R.W. Long) Sundberg, Sida 21:905. 2004. TYPE: U.S.A. FLORIDA.

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